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Identifying optimal sites for natural recovery and restoration of impacted biogenic habitats in a special area of conservation using hydrodynamic and habitat suitability modelling

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Abstract

Selection of sites for successful restoration of impacted shellfish populations depends on understanding the dispersion capability and habitat requirements of the species involved. In Strangford Lough, Northern Ireland, the horse mussel (*Modiolus modiolus*) biogenic reefs cover only a fraction of their historical range with the remaining reefs badly damaged and requiring restoration. Previous experimental trials suggest that translocation of horse mussels accelerate reef recovery and has therefore been proposed as a suitable restoration technique. We used a series of coupled hydrodynamic and particle dispersal models to assess larval dispersion from remnant and translocated populations to identify suitable areas for adult live *M. modiolus* translocation in Strangford Lough, Northern Ireland. A maximum entropy model (MAXENT) was used to identify if dispersing larvae could reach habitat suitable for adult *M. modiolus*. From these we predicted if translocated mussels will reseed themselves or be able to act as larval sources for nearby reefs. The dispersal models showed that the remnant *M. modiolus* populations are largely self-recruiting with little connectivity between them. The majority of larvae settled near the sources and movement was largely dependent on the tides and not influenced by wind or waves. Higher reef elevation resulted in larvae been able to disperse further away from the release point. However, larval numbers away from the source population are likely to be too low for successful recruitment. There was also little connectivity between the Irish Sea and Strangford Lough as any larvae entering the Lough remained predominantly in the Strangford Narrows. The areas covered by these self-seeding populations are suitable for *M. modiolus* translocation according to the MAXENT model. As a result of this work and in conjunction with other field work we propose a combination of total protection of all remaining larval sources and small scale translocations onto suitable substrata in each of the identified self-recruiting areas.

Keywords: biogenic reefs; connectivity; larval dispersal; habitat restoration; marine reserves; *Modiolus modiolus*

1. Introduction

Mussels act as keystone species by increasing habitat complexity (Koivisto and Westerbom, 2010), providing a wide range of ecosystem services (Coen et al., 2007) and stabilising the seabed (Jones, 1951; Rees, 2009). Removal of mussels results in a reduction of habitat complexity (Cranfield, 2004; Rees et al., 2008; Seed and Suchanek, 1992; Wildish et al., 1998). Increased fragmentation from anthropogenic impact can result in low connectivity between the local subpopulations leading to loss of sources of larvae and recruitment limitation in the metapopulation sinks (Kritzer and Sale, 2004; Kinlan et al., 2005; Lipcius et al., 2008; Mann and Evans, 2004). Therefore, without intervention, regeneration of these biogenic habitats may be slow or simply never occur. Factors affecting the length of time taken for the natural regeneration of biogenic reefs include the period of non-disturbance, proximity of propagule sources (Cranfield et al., 2004) and hydrodynamic influences on propagule dispersal (Ayata et al., 2009). In addition, suitable habitat for keystone species has to be available for the regeneration process to start (Caddy and Defeo, 2003).

To date most restoration programmes for bivalves have focused on freshwater mussels, oysters, clams and cockles (e.g. Lundquist et al., 2009; Schulte et al., 2009; Wilson et al., 2011). Key elements of shellfish restoration are to predict the location and likelihood of natural recovery at impacted sites and to identify sites where intervention is most likely to succeed. The present paper was stimulated by attempts to restore impacted reefs of a marine mussel, *Modiolus modiolus*, in a Special Area of Conservation (SAC).

M. modiolus is a widely distributed boreal species extending from southern parts of the White Sea as far south as the southern Irish Sea (Rees, 2009) and may form complex biogenic reefs. The reefs can be semi-infaunal or infaunal extending from the lower shore to over 100 m depth (Holt et al., 1998; Tendal and Dinesen, 2005). Although *M. modiolus* is adapted to living buried in the sediment (Meadows and Shand, 1989), it requires some hard substratum for byssus attachment. It can be found in a wide variety of substrata, living epifaunally in rocky bottoms (Ojeda and Dearborn, 1989; Rowell, 1967; Witman, 1987) and on pylons of offshore structures (Anwar et al., 1990). In Europe *M. modiolus* is usually found living in gravels and coarse substrata and soft muds with some shell fragment (Comely, 1978; Mair et al., 2000; Roberts et al., 2011).

In the 1970s large areas of the sea bed in Strangford Lough, Northern Ireland, were characterised by biotopes dominated by *M. modiolus* (Erwin, 1977) and Strangford Lough was designated as the UK's third Marine Nature Reserve and is listed as a NATURA 2000 area [UK0016618] (JNCC, 2012) and has been identified as a pilot Marine Protected Area (MPA) (Cork et al., 2006). A key feature in these designations was the presence of biogenic reefs of *M. modiolus* (DOENI, 1994; Roberts et al., 2011). However, as a result of impacts from benthic fishing in the 1980s *M. modiolus* communities showed dramatic declines in diversity and distribution in Strangford Lough (Roberts et al., 2011, 2004; Service and Magorrian, 1997; Strain et al., 2012).

The most recent surveys (Roberts et al., 2011) reported that the remnant *M. modiolus* metapopulation is fragmented into several subpopulations at sites in the central section of Strangford Lough (Fig. 1). Currently these remnant *M. modiolus* populations support communities ranging from those with high diversity and high recruitment to those where diversity and recruitment are low. This reflects whether the mussels are present in continuous large or small fragmented clumps or isolated groups (Roberts et al., 2011).

Preliminary restoration trials, involving translocation of 6000 mussels on to an artificial reef made from shell cultch were initiated in 2010 (Fariñas-Franco et al., 2012), using techniques recommended for oyster restoration (Nestlerode et al., 2007; Schulte et al., 2009). Selection of the site for the restoration trial was based on published guidelines (Brumbaugh et al., 2006; Fariñas-Franco et al., 2012). However, it is now recognised that an understanding of the mechanisms and patterns of propagule dispersal and habitat requirements of impacted keystone species is essential to optimize restoration strategies and the design and designation of protected areas (Gibson et al., 2004; Levin, 2006).

Hydrodynamic models are increasingly used to predict spatial and temporal variability in larval dispersal and settlement and to identify whether restoration sites are likely to act as sources or sinks of larvae or both (Ayata et al., 2009; Lundquist et al., 2009; Newell et al., 2010; Yang et al., 2010). These numerical simulations generally involve combined 3-D hydrodynamic and particle tracking models often with different tide and wind scenarios (Lundquist et al., 2009). Habitat suitability mapping is also frequently used to identify areas in need of restoration or preservation (Gibson et al., 2004), or identify candidate areas in species reintroduction programs (Olsson and Rogers, 2009; Wilson et al., 2010). Predictive species-specific landscape favourability models, based on Geographic Information Systems (GIS), have become the favoured method in defining species habitat requirements (Guisan and Zimmermann, 2000; Wilson et al., 2011).

According to Levin (2006) the two most important questions in larval dispersal studies are "Where do larvae go?" and "Where do they come from?" A third question may be added when larval dispersal studies are used to predict where impacted communities are likely to recover naturally or to identify optimal sites for restoration: "Does suitable habitat exist at sites which are major larval sinks?". This paper addresses these three questions by using hydrodynamic modelling to predict larval dispersal and connectivity between remaining sources of larvae and a habitat suitability model for *M. modiolus* in an enclosed sea Lough. This will enable us to predict where natural recovery is most likely and to select optimal sites for intervention involving habitat restoration and translocation of mussels.

2. Study area and methods

2.1 Study area

Strangford Lough is a large marine inlet of the Irish Sea located between 54.36° N 5.43° W and 54.20° 5.30° W in the northeast coast of Ireland (Fig. 1). It is 29 km long and 8 km wide at its widest point covering an area of 150 km^2. The Lough is almost completely enclosed, only connected to the Irish Sea by an 8 km long and 1 km wide channel (Strangford Narrows) with strong currents of up to 3.5 m s^{-1} (Magorrian et al., 1995). In the Strangford Narrows the average tidal range is 3.6 m (O'Rourke, 2010), with ranges inside the Lough between 3.5 m at mean spring tides and 2 m at neaps (Davison and Boaden, 1990) with a flushing time estimated to be 1.6 days (Service et al., 1996). Earlier reports describe Strangford Lough as being divided into two basins, one north and one south of Long Sheelah (Fig. 1). Hydrographic characteristics of the two basins differ; water in the north basin is retained for longer periods than in the southern basin, which mixes more freely with the Irish Sea (Boyd, 1973).

2.2 Hydrodynamic model

The hydrodynamics of Strangford Lough were numerically predicted using the Strangford Lough current and wave models (Kregting and Elsäßer, 2012) in order to provide a consistent comparative measure of current and wave conditions between sites. Using MIKE 21 modelling software (DHI Water and Environment software package; www.dhisoftware.com) both models were setup using the same flexible mesh (FM) technology. The hydrodynamic model uses a finite volume method determining the current field by solving a depth averaged shallow water approximation, whereas the wave model simulates the sink and source terms of a WAM cycle 4 spectral wave model in quasi steady mode. Earlier studies suggest that in Strangford Lough *M. modiolus* may release small numbers of gametes through the year (trickle spawning) (Brown, 1984; Seed and Brown, 1975) but recent studies (Fariñas-Franco and Roberts in prep.) suggest that gamete release may peak slightly in autumn in some sub-populations. In addition, from the laboratory observations the minimum planktonic phase for *M. modiolus* larvae in Strangford Lough is 34 days with most larvae settling after 56 days (Fariñas-Franco and Roberts in prep.). Therefore the hydrodynamic models were run from September to October 2010 for 56 days incorporating 4 neap and 4 spring cycles. Development, calibration and performance of the model with an approximate cell size of 50 m in the areas of interest can be found in Kregting and Elsäßer (2012).

2.3 Simulation of larval release and dispersal

Spawning was simulated at four extant *M. modiolus* populations in Strangford Lough: Hadd Rock in the North Basin; Craigyouran and Round Island Pinnacle in the South Basin, Eastern shore and Black Rock in the South Basin, Western shore (Fig. 1). Particle release was also simulated from the restoration site to assess its potential to enhance larval dispersal within the Lough. Further, to evaluate the potential larval import from *M. modiolus* populations outside Strangford Lough, particles were released as a diffuse source from the Irish Sea.

Larval dispersal was simulated using the MIKE 21 particle tracking module coupled to the hydrodynamic model. For each location 200 particles were released every 5 minutes simulating a trickle-spawning reproductive behaviour. Zero sinking velocities were assumed for the particles. The particle tracking module applied in this study represents the simulated movement of larvae by applying a random walk procedure in two dimensions using the Langevin equation to simulate both diffusion and advection (Pope, 2000). While the initial hydrodynamic conditions were derived as depth averaged velocities, in the particle tracking model a logarithmic velocity profile was used to estimate the change in velocity with depth. The bed friction velocity to derive the logarithmic profile is directly calculated in the hydrodynamic model. Recent measurements at the sites have shown that a logarithmic profile is appropriate and that for the given period stratification is limited. Fresh water inflows are limited compared to the tidal exchange on each ebb flood cycle and thermal layering is if at all limited to the summer months. CTD surveys of the Lough have shown (Taylor and Service, 1997; Fariñas-Franco, unpublished data) that the water column is well mixed. Turbulence intensity in the Lough, in particular closer to the Narrows is slightly elevated due to residual turbulence originating from the high inflow velocities at the Narrows. Anecdotal evidence suggests considerable eddying around the various pladdies and islands. This supports the observation of a high degree of mixing in the Lough. To represent this effect a slightly raised diffusion coefficient of 1.1 instead of the recommended value of 1.0 was used in the particle tracking simulations to account for the sub grid scale diffusion in the model where the diffusion coefficient describes the transport of the particles by molecular scale diffusion and non-resolved turbulence or eddies (DHI, 2011; Rodi, 1993).

Vertical diffusion was derived using a separate diffusion coefficient formulation. This allowed particles to be dispersed vertically in the water column. In all simulations it was assumed that the gametes are released above the laminar sublayer. Since settling was not enabled in the model, only particles reaching the bed as a result of the vertical diffusion are considered to settle on the bed. At this point re-suspension of the particle was suppressed in the model and settled particles were held until the end of the simulation.

While it is possible to simulate migratory and settlement strategies in the numerical model, these would be solely hypothetical as at present we do not have sufficient information to support them. In essence there is no published data on larval dispersal or settlement behaviour for *M. modiolus,* thus in the present study a conscious decision was made to simulate larval dispersal and settlement using neutrally buoyant inert particles and assume the end point to be where the particles reached the bed.

In the wind drift simulations the wind velocities 10 metre above mean sea level derived from wind observations made at Orlock Point, around 20 km north of the northern end of

Strangford Lough at the entrance to Belfast Lough, were used. To take account of the change in atmospheric boundary layer, both due to difference in surrounding terrain and elevation of the measurement station, a conversion was obtained (Kregting and Elsäßer, 2012). In the particle tracking model a parabolic drift profile was derived to account for the change in wind drift with depth.

As mentioned above a simulation period of 56 days was used to run the particle tracking model. As the dispersion pattern is unknown at the start, a sufficient period has to pass from the start of the simulation to derive a pseudo stationary pattern for the settled particles. Therefore only the last fortnight of the simulation period was used to derive the figures shown in the paper (Fig. 5) ensuring that short term variations in relation to neap and spring tides are accounted for, yet the concentrations shown are commensurate to typical variations in flow conditions. At each time step the number of particles on the bed per square meter was represented in relation to the total number of larvae released in the model to this point. This derived an average density of particles reaching the bed per square meter per 1 million particles released from each site. Most particles released in the last 14 days of the simulation do not influence the output of the model because they are still in the water column.

Reef elevation is considered advantageous in shellfish restoration programs (Schulte et al., 2009). Therefore simulations using a release point at four different heights above the seabed (0.1, 0.25, 0.5 and 1 m) were carried out at an experimental *M. modiolus* reef deployed as part of the *Modiolus* Restoration Plan (Roberts et al., 2011) to establish the most efficient artificial reef design. The simulation was carried out for 56 days and the number of particles reaching areas 150 and 300 metres North and South of the release point was calculated.

2.4 Habitat suitability model

2.4.1 Landscape and habitat parameterisation

Although many historical records exist for *M. modiolus* in Strangford Lough, it was decided to limit the species presence records to the most up-to-date distributional data. The distribution of *M. modiolus* in Strangford Lough was determined by means of an extensive survey carried out between 2008 and 2010 using Remotely Operated Vehicles (ROV) and SCUBA diving. *M. modiolus* was recorded at 124 out of over 400 sites surveyed (Roberts et al., 2011). Where *M. modiolus* occurred, depth (in metres) and substratum characteristics (percentage cover) were recorded because they reflect the environmental parameters such as water movement and sedimentation most relevant to its current distribution. Because the loss of *M. modiolus* could have caused a change in substratum over time, historical data were excluded as they may be less biologically relevant to current conditions within the Lough. Other environmental parameters such as temperature and salinity were excluded because they were not considered to be sufficiently site specific.

Point data on substrate type percentage cover and depth were interpolated using the Inverse Distance Weighted (IDW) interpolation tool in the Spatial Analysis toolbox in ESRI®ARCGIS v10.0™ (ESRI, California, USA). ArcGIS v10.0™ was used to extract habitat variables on a landscape scale resampled to a common pixel size of 40 m throughout Strangford Lough.

2.4.2 Statistical analyses

The maximum entropy model (MaxEnt) was selected for the present study because it provides a straightforward mathematical formulation to model the distribution of species based on presence only data and available habitat variables. MAXENT 3.2.1a (Phillips et al., 2006; Phillips and Dudlik, 2008) was used to predict the probability of *M. modiolus* occurrence at a pixel size of 40 m. Due to the restricted range of *M. modiolus* it was hypothesised that the species' habitat associations would occupy a narrow band of tolerance and, therefore, not display linear relationships. Consequently, model flexibility was maximised by considering quadratic, product, threshold, hinged and discrete functions for all habitat parameters (Phillips and Dudlik, 2008). Jackknife resampling analysis was used to determine a heuristic estimate of the relative contribution of each variable based on the performance of the global model (known as test gain) without the variable of interest compared to the influence of that variable in isolation (derived from a univariate model only). Global model performance was judged using the area under the curve (AUC) in the receiver operating characteristic (ROC) analysis (Liu et al., 2005). The ROC curve is calculated by plotting *sensitivity* against *1-specificity* (Phillips et al. 2006). The AUC can be interpreted as the probability that a random positive record and a random negative record for the species modelled are correctly ordered by the classifier and is, therefore, an indication of global model performance (Phillips and Dudlik, 2008). Model significance was tested using a one-tailed binomial test of omission (the fraction of test occurrence falling outside the prediction) under the null hypothesis of random prediction, given the same fractional predicted area. Marginal response curves of the predicted probability of species occurrence were graphed for each explanatory variable that contributed substantially to the global model. A map of habitat favourability for *M. modiolus* was generated to reflect the predicted probability of species occurrence using ESRI®ArcGIS v10.0™.

Model testing was carried out for MaxEnt model containing species presence records using a test set of 25% of presence records. The fit of the model to the test data is the real test of the models predictive power using the AUC value. The overall sensitivity of the model is considered satisfactory if AUC is above 0.75 (Phillips and Dudlik, 2008).

3. Results

3.1 Particle dispersal.

There were very high levels of particle retention close to the release points at four natural sites and the artificial reef after 56 days of continuous release; highest densities of particles were recorded within 500 metres of the origin (Figs. 2, 3). Remaining particles were dispersed along the direction of the main tidal flow (Figs. 2, 3) although densities were at least 1 order of magnitude lower than near the release.

3.1.1 Connectivity between Strangford Lough and the Irish Sea.

Highest densities of particles imported from the Irish Sea were observed close to the shoreline in the Strangford Narrows with estimated accumulations of between 0.5 and 1 m^2 10^{-6} released reaching as far as Ballyhenry Island (Fig. 2A). Although particles could reach areas within the historical distribution range of *M. modiolus* in the south basin, very few were transported past Long Sheelah into the Northern Basin and none of the scenarios exported significant amounts of particles beyond the model boundaries. Particles were also flushed from release sites in both the south and north basins to the narrows and potentially out of the Lough although in extremely low concentrations (< 0.002 m^{-2} 10^{-6} released) (Figs. 2B - D), compared with the level of retention observed at each release site.

3.1.2 Connectivity between sites within Strangford Lough.

The majority of particles released from Black Rock (Fig. 2B) and the restoration site (Fig. 3A), on the West section of the Lough remained near the sources and accumulated in a North/South direction. Existing populations in Ringhaddy Sound are likely to have strong connectivity with these beds. However, the model suggested little indication of connectivity between beds on the western side of the Lough and those near Hadd Rock in the North and Craigyouran and Round Island Pinnacle in the East (Figs. 2B-E). Wind has very little influence on particle dispersal at the release sites due to the water depth. As a representative test case particles were released from Black Rock under tide driven dispersal and combined wind and tide driven dispersal. Results showed little difference with scenarios incorporating wind forcing from the West (Figs. 2B - C). In both cases higher densities of particles were observed close to the sources with most dispersal occurring in a North-South direction. However, the wind slightly reduced retention and forced more particles to travel further in an Easterly and North-Easterly direction. Additional dispersal due to wave action was two orders of magnitude lower than at the near shore shallow site (Fig. 4).

Particles released from remnant mussel populations at more easterly points in the Lough (Craigyouran and Round Island Pinnacle) also tended to accumulate in high densities near their release points (> 2 m^2 10^{-6} released) with lower densities travelling with the current along the edge of the main channel. There was negligible connectivity with the Hadd Rock beds in the North or the Black Rock and the restoration site in the South (Fig. 2E). Highest densities of particles released from Hadd Rock remained close to the source. The overall dispersal pattern followed a North-West to South direction with particle concentrations of 2 orders of magnitude lower reaching as far as Maghee Island in the North and the Black Rock and the restoration site in the South. Some particles were transported towards the Green Island Passage, a historic bed where horse mussels used to be found.

3.1.3 Effect of elevation on particle dispersal at the artificial reef

The patterns of particle dispersal did not show the postulated expansion as a result of increasing height of the source. Model results showed high concentrations of particles very close to the restoration site following a North-South plume (Figs. 3A - D). Concentrations of deposited particles showed a decreasing trend with reef elevation at the release site. At 150 and 300 m North and South from the release point concentrations increased with increasing release height (Fig. 5). The effect of elevation was negligible at distances over 300 m as concentrations were below two orders of magnitude compared to those at the release site.

3.2 Habitat suitability modelling

The one-tailed binomial test was highly significant ($P < 0.001$), indicating the model successfully predicts occurrence records significantly better than random (Anderson, 2003). Model performance, defined as the area under the curve, was highly discriminative with AUC = 0.965, indicating that *M. modiolus* occupied a highly specific habitat, in terms of depth and substrata. Test AUC was 0.943 indicating a good model fit. At the broad ecological scale, *M. modiolus* occurrence was most strongly associated with depth, explaining 48.94% of the variation in the distribution of *M. modiolus*, where the probability of occurrence peaked ≈ 30 metres (Fig. 6). *M. modiolus* presence was positively associated with mud and sand substrata explaining 5.99% and 3.80% of the variation in distribution, respectively, with the probability of species occurrence close to 1 when the percentage cover of finer substrata was close to 100% (Fig. 7). However, *M. modiolus* occurrence was negatively associated with cobbles, boulders, gravel, bedrock and pebbles, explaining 17.98%, 9.80%, 5.14 %, 4.36% and 3.94% of the variation in distribution, respectively (Fig. 6). The probability of *M. modiolus* occurrence was virtually zero where the percentage cover of these coarser substrata was high (Fig. 7). Current habitat suitability for *M. modiolus* based on the MAXENT model is largely biased towards the mid region of Strangford Lough (Fig. 8A) reflecting the best estimated hindcast of its historical distribution (Fig. 8B).

4. Discussion

Many species of benthic marine invertebrates produce planktonic larvae for dispersal. Early developmental stages tend to migrate upwards to facilitate dispersal whereas later developmental stages move downwards or sink prior to settlement and attachment. Vertical migration of some species of larvae is affected by environmental cues including temperature, salinity, light and state of tide (see for examples (Knights et al., 2006; Robins et al., 2012) which enable larvae to exploit local hydrographic conditions such as axial convergent fronts in estuaries to ensure that they increase the chances of reaching suitable habitat (Robins et al., 2012). Similarly, Knights et al. (2006) found that larvae of blue mussel (*Mytilus edulis*) species were distributed homogeneously throughout the water column during flood tides but lower in the water column during ebb tides resulting in net transport in the direction of the flooding tide.

In tidal and fluvial environments vertical dispersion of particles is a key process solely driven by the turbulence acting in the vertical direction. In most instances it is governed by the bed related boundary layer developing throughout the water depth and thus primarily characterised by u* (the shear velocity, a function of bed roughness and mean horizontal current magnitude) and the water depth (h). In addition, obstacles such as islands, bed forms, sudden changes in depth, jets from fluvial inflows or narrowing of bathymetry can also give rise to additional turbulence. Although we are not particularly concerned about its origins, it is important to recognise that turbulence is the key driver for vertical dispersion of particles in the coastal environment.

This vertical dispersion often overcomes density differences between suspended particles and the ambient water and hence can inhibit settling almost completely. In the Strangford Lough environment turbulence intensity significantly increases with slacking of the tide indicating a significant amount of residual turbulence right throughout the tidal cycle (Kregting and Elsäßer, 2012). Observations show high turbidity levels for days after large local wave events in the Lough (Fariñas-Franco, unpublished raw data). This in fact means that small solid particles with densities in excess of twice the seawater may remain suspended for several days solely due to the ambient turbulence in the water. In relation to larval dispersal, small density differences seen between the larvae and the seawater are essentially overcome by the inherent turbulence in the water column. A number of authors have observed larval migration with the velocity scales of swimming larvae in the range of 1.5 –

10 mm s^{-1} (e.g. (Hidu and Haskin, 1978; Mann and Wolf, 1983; McDonald and Grünbaum, 2010; Mileikovsky, 1973). However, because these are orders of magnitude lower than background turbulence in Strangford Lough, where flow velocities reach over 3 m s^{-1} (Kregting and Elsäßer, 2012), we believe using a particle tracking model which simulates both diffusion and advection but assumes zero sinking velocities or swimming speeds provides us with realistic outputs of larval dispersal in Strangford Lough. When the model was run at different release heights, which effectively simulates both the effects of reef elevation and vertical upward migration of larvae, there was minimal effect on particle dispersal range (Fig. 3).

According to Stokes law settlement velocity is proportional to the diameter squared so that a negatively buoyant particle with twice the diameter and the same density as a smaller particle has four times the settling velocity. Thus the settling velocities of larvae will increase as they grow. In addition, it has been suggested that mytilid larvae settle preferentially on conspecific byssus (Ompi, 2010) and settlement of *M. modiolus* larvae is thought to be highly dependent on the presence of clumped live mussels (Rees, 2009; Roberts et al., 2011).

4.1 Particle dispersal and connectivity of M. modiolus *populations*

To simulate trickle spawning in *M. modiolus* this study was based on continuous particle release over 56 days incorporating all stages of the tides in contrast to other studies which involved instantaneous release of particles. Particle dispersal patterns from each of the extant *M. modiolus* sources, including the artificial reef site, revealed very high levels of particle retention near the sources and low densities of particles being exported outside the model boundaries. Wind and wave action play an insignificant role in the dispersal and a minor role in the advection of the larvae. This is not surprising given that the closure depth in the Lough is around 0.5m below low water level (depth to which littoral transport is of significance, see

Mangor (2004). However this makes this scenario different from a large number of other dispersal scenarios for mussels for two reasons: The Lough is protected from long period waves with the open water fetch length in the order of 15km, thus resulting in a wave period limit of 4-5sec and insignificant penetration of waves from the Irish Sea (JONSWAP). Secondly *M. modiolus* generally occurs in water depths greater than 5 m below Chart Datum (Holt et al., 1998), thus directly only affected by currents which penetrate the full water column.

The high near-source retention of particles predicted by the model is supported by data showing high natural recruitment at all the extant populations except for Hadd Rock in the North Basin (Fariñas-Franco, unpublished raw data). Dispersal of particles released from sites within the Lough followed the direction of the main tidal flow along predominantly north-south axes (Figs. 2, 3). There was negligible transfer of particles in an east-west/west-east direction across the main tidal flow. This suggests low connectivity between the remaining reefs. Similarly the model suggested that there was little particle transfer to and from outside the Lough (Fig. 2A). However, the model did predict hotspots of particle retention at a number of locations in the Narrows, particularly on the eastern side from a site outside the Lough (Fig. 2A). This prediction is supported by the presence of isolated individuals of *M. modiolus* (D. Roberts, personal observation) along the eastern side of the Narrows.

4.2 Habitat suitability

The habitat suitability model developed in this study, which was based on ROV and SCUBA surveys carried out between 2008 and 2010 indicated that extant remnant populations of *M. modiolus* are highly correlated with deep areas of soft substrata within the central region of Strangford Lough. Depth in particular is a key indicator in the distribution of *M. modiolus* with the probability of predicting its distribution being much higher at depths of

-20 to -40 metres, than at shallower or deeper areas (Fig. 7). Nonetheless, substratum has a key role in the distribution of this species with strong negative relationships between coarser substratum types, such as bedrock, boulders and cobbles, and positive relationships between softer finer substrata, such as sand and mud (Figs. 6 & 7). Similarly, generalized additive models (GAM) developed by Ragnarsson and Burgos (2012) also indicated a significant negative correlation existed between substrate coarseness (i.e. stone coverage) and the abundance of *M. modiolus* in South-West Iceland.

In our model predictions, the distribution of *M. modiolus* showed considerable overlap with distributional estimates based on historical data (Figs. 8 A, B) and with those based on video and acoustic surveys carried out between 1990 and 2003 (Roberts et al., 2004; Service and Magorrian, 1997). These authors identified a number of different habitats, including those where *M. modiolus* densities were high and those characterised by shell debris where *M. modiolus* had been heavily impacted by trawling. However, marked changes in sediment composition may lead to the establishment of a different community (Service and Magorrian, 1997). Indeed, historical impacts on *M. modiolus* populations in Strangford Lough's North Basin may have reduced them to levels from which recovery is not possible (Roberts et al., 2011; Strain et al., 2012).

4.3 Recovery and restoration

The presence of mud with shell affords the potential for settlement and natural recovery. Natural recovery is dependent on both local hydrodynamic conditions for dispersal of propagules and the availability of suitable habitat for settlement. The particle dispersal models presented in this paper suggest that there is little connectivity between the remnant populations, including the restoration site, in Strangford Lough and that the *M. modiolus* metapopulation in the Lough is now fragmented into isolated sub-populations. Population data suggest that these may or may not be self-replenishing. Poor recruitment and no apparent reproductive activity (Fariñas-Franco and Roberts, in prep.) suggest that populations in the North Basin , which are dominated by larger (older) individuals and have few mussels smaller than 5 cm , may be suffering density-related Allee effects (Allee, 1931) which, together with poor connectivity with other populations, compromise their long-term viability and potential for recovery. That the early growth stages of *M. modiolus* are subject to high predation is implicit in the escape through growth model of Seed and Brown (1978). Early settlement stages are thought to gain some protection from predation if they settle within the byssal matrix of a mussel bed (Holt et al., 1998; Rees, 2009; Witman, 1985).

Consequently although the habitat suitability model indicates that an extensive area of potentially suitable habitat for adult *M. modiolus* remains, it does not indicate the likelihood of spat recruitment which probably depends on the presence of relatively dense patches of live mussels. Fariñas-Franco et al. (2012) found enhanced *M. modiolus* spat recruitment amongst clumps of conspecifics. Restoration involving restocking the areas identified as suitable by both models will increase recruitment on existing and transplanted areas but high predation will limit the reseeding success of areas where *M. modiolus* beds have disappeared altogether. It is very likely that the establishment of new larval sources will not help restoring areas which have lost all their *Modiolus* reefs such as Green Island Passage and North Ringhaddy Sound if these areas are not restocked as well.

5. Conclusions

This study has demonstrated that remnant populations of *Modiolus modiolus* in Strangford Lough, an enclosed embayment off the Irish Sea, are largely self-recruiting with little connectivity between them and with populations outside the lough. We therefore suggest that the best approach to accelerate the recovery and restoration of *M. modiolus* biogenic reefs in Strangford Lough is to provide total protection of all remaining larval sources and establish additional patches of mussels in areas where the models simulated above predict between 0.02 and 0.05 particles (larvae) m^{-2} 10^{-6} released. Such patches of mussels should be sourced within the immediate vicinity but should not require a cultch foundation (see Fariñas-Franco et al., 2012). This would increase connectivity and suitable habitat for juveniles and thus start to overcome the main bottlenecks to recovery (see for example Caddy and Defeo 2003 and references therein). This study like many others (Brumbaugh and Coen, 2009; Coen and Luckenbach, 2000; Coen et al., 2007; Lenihan, 1999; Powers et al., 2009) has shown that recovery of bivalve biogenic reefs is slow and complex. In areas where natural recovery of endangered marine species which reproduce by gamete broadcast and planktonic development seems unlikely, intervention should not be carried out before undertaking hydrodynamic and habitat suitability modelling to ensure that restoration sites are located where recovery has the highest likelihood of success.

5. Acknowledgments

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References

Allee, W., 1931. *Animal aggregations: a study in general sociology*. University of Chicago Press, Chicago.

Anderson, R., 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling, 162, 211–232.

Anwar, N.A., Richardson, C. A., Seed, R.,1990. Age determination, growth rate and population structure of the horse mussel *Modiolus modiolus*. Journal of the Marine Biological Association of the United Kingdom, 70, 441–457.

Ayata, S., Ellien, C., Dumas, F., Dubois, S., 2009. Modelling larval dispersal and settlement of the reef-building polychaete *Sabellaria alveolata*: Role of hydroclimatic processes on the sustainability of biogenic reefs. Continental Shelf Research, 29, 1605–1623.

Boyd, R., 1973. The relation of the plankton to the physical, chemical and biological features of Strangford Lough, Co. Down. In: Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science, 73, 317–353.

Brown, R.A., 1984. Geographical variations in the reproduction of the horse mussel, Modiolus modiolus (Mollusca: Bivalvia). Journal of the Marine Biological Association of the United Kingdom, 64, 754-770.

Brumbaugh, R.D., Beck, M.W., Coen, L.D., Craig, L., Hicks, P., 2006. A practitioner's guide to the design and monitoring of shellfish restoration projects: an ecosystem services approach. The Nature Conservancy, Arlington, VA.

Brumbaugh, R.D., Coen, L.D., 2009. Contemporary approaches for small-scale oyster reef restoration to address substrate versus recruitment limitation: a review and comments relevant for the Olympia oyster, *Ostrea lurida* Carpenter 1864. Journal of Shellfish Research, 28, 147–161.

Caddy, J.F., Defeo, O., 2003. Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources. FAO Fisheries Technical Paper. Food and Agriculture Organization of the United Nations, Rome.

Chia, F., 1984. Locomotion of marine invertebrate larvae: a review. Canadian Journal of Zoology, 62, 1205–1222.

Coen, L.D., Brumbaugh, R.D., Bushek, D., Grizzle, R., Luckenbach, M., Posey, M.H., Powers, S.P., Tolley, S.G., 2007. Ecosystem services related to oyster restoration. Marine Ecology Progress Series, 341, 303–307.

Coen, L.D., Luckenbach, M., 2000. Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation? Ecological Engineering, 15, 323–343.

Comely, C., 1978. *Modiolus modiolus* (L.) from the Scottish west coast. I. Biology. Ophelia, 17, 167–193.

Cork, M., Adnitt, C., Staniland, R., Davison, A., 2006. Creation and Management of Marine Protected Areas in Northern Ireland. Environment and Heritage Service Research and Development Series. No. 06/18. Environment and Heritage Service, Belfast.

Cranfield, H.J., 2004. Macrofaunal assemblages of benthic habitat of different complexity and the proposition of a model of biogenic reef habitat regeneration in Foveaux Strait, New Zealand. Journal of Sea Research, 52, 109–125.

DHI, 2011. MIKE 21 & MIKE 3 flow model FM. Particle tracking module. Scientific documentation. DHI Water and Environment, Hørsholm.

DOENI., 1994. Strangford Lough proposed Marine Nature Reserve. Guide to designation. HMSO, Belfast.

Davison, A.J., Boaden, P.J.S., 1990. The management of Strangford Lough: a study of the marine environment, its conservation and its exploitation. Queen's University Belfast, Belfast.

Erwin, D., 1977. A diving survey of Strangford Lough: the benthic communities and their relation to substrate: a preliminary account. In: Keegan, B., Ó Céidigh, P., Boaden, P.J.S. (Eds.), Biology of Benthic Organisms: 11th European Symposium on Marine Biology, Galway, October 1976. Pergamon Press, Oxford, pp. 215–224.

Fariñas-Franco, J.M., Allcock, L., Smyth, D., Roberts, D., 2012. Community convergence and recruitment of keystone species as performance indicators of artificial reefs. Journal of Sea Research (in press).

Gibson, L., Wilson, B.A., Cahill, D.M., Hill, J., 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS based approach. Journal of Applied Ecology, 41, 213–223.

Guisan, A. and Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling, 135, 147–186.

Hidu, H. and Haskin, H.H., 1978. Swimming speeds of oyster larvae *Crassostrea virginica* in different salinities and temperatures. Estuaries and Coasts, 1, 252–254.

Holt, T.J., Rees, E.I., Hawkins, A.J.S., Seed, R., 1998. Biogenic Reefs (volume IX). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science (UK Marine SACs Project).

JNCC, 2012. Strangford Lough Special Area of Conservation http://jncc.defra.gov.uk/protectedsites/sacselection/sac.asp?EUCode=UK0016618

Jones, N.S., 1951. The bottom fauna off the South of the Isle of Man. The Journal of Animal Ecology, 20, 132–144.

Kinlan, B.P., Gaines, S.D., Lester, S.E., 2005. Propagule dispersal and the scales of marine community process. Diversity and Distributions, 11, 139–148.

Knights, A., Crowe, T. and Burnell, G., 2006. Mechanisms of larval transport: vertical distribution of bivalve larvae varies with tidal conditions. Marine Ecology Progress Series, 326, 167–174.

Koivisto, M.E., Westerbom, M., 2010. Habitat structure and complexity as determinants of biodiversity in blue mussel beds on sublittoral rocky shores. Marine Biology 157, 1463–1474.

Kregting, L.T., Elsäßer, B., 2012. Strangford Lough model calibration report. Unpublished report.Queen's University Belfast, Belfast.

Kritzer, J.P., Sale, P.F., 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries 5, 131–140.

Lenihan, H.S., 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs, 69, 251–275.

Levin, L. A., 2006. Recent progress in understanding larval dispersal: new directions and digressions. Integrative and comparative biology, 46, 282–97.

Lipcius, R.N., Eggleston, D.B., Schreiber, S.J., Seitz, R.D., Shen, J., Sisson, M., Stockhausen, W.T., Wang, H. V., 2008. Importance of Metapopulation Connectivity to Restocking and Restoration of Marine Species. Reviews in Fisheries Science, 16, 101–110.

Liu, A., Schistermana, E.F., Wu, C., 2005. Nonparametric estimation and hypothesis testing on the partial area under receiver operating characteristic curves. Communications in Statistics— Theory and Methods, 34, 2077–2088.

Lundquist, C., Oldman, J.W., Lewis, M.J., 2009. Predicting suitability of cockle *Austrovenus stutchburyi* restoration sites using hydrodynamic models of larval dispersal. New Zealand Journal of Marine and Freshwater Research, 43, 735–748.

Lundquist, C., Thrush, S., 2004. Limited transport and recolonization potential in shallow tidal estuaries. Limnology and Oceanography, 49, 386–395.

Magorrian, B.H., Service, M., Clarke, W., 1995. An acoustic bottom classification survey of Strangford Lough, Northern Ireland. Journal of the Marine Biological Association of the United Kingdom, 75, 987–992.

Mair, J., Moore, C., Kingston, P., 2000. A review of the status, ecology and conservation of horse mussel *Modiolus modiolus* beds in Scotland. Scottish Natural Heritage Commissioned Report No. F99PA08. Scottish Natural Heritage, Edinburgh.

Mangor, K., 2004. Shoreline Management Guidelines. DHI Water and Environment, Hørsholm.

Mann, R., Evans, D.A., 2004. Site selection for oyster habitat rehabilitation in the Virginia portion of the Chesapeake Bay: A commentary. Journal of Shellfish Research 23, 41–49.

Mann, R., Wolf, C.C., 1983. Swimming behavior of larvae of the ocean quahog *Arctica islandica* in response to pressure and temperature. Marine Ecology Progress Series, 13, 211–218.

McDonald, K.A., Grünbaum, D., 2010. Swimming performance in early development and the "other" consequences of egg size for ciliated planktonic larvae. Integrative and Comparative Biology, 50, 589–605.

Meadows, P.S., Shand, P., 1989. Experimental analysis of byssus thread production by *Mytilus edulis* and *Modiolus modiolus* in sediments. Marine Biology, 101, 219–226.

Mileikovsky, S., 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. Marine Biology, 23, 11-17

Nestlerode, J., Luckenbach, M., O'Beirn, F.X., 2007. Settlement and survival of the oyster *Crassostrea virginica* on created oyster reef habitats in Chesapeake Bay. Restoration Ecology, 15(2), 273–283.

Newell, C.R., Short, F., Hoven, H., Healey, L., Panchang, V., Cheng, G., 2010. The dispersal dynamics of juvenile plantigrade mussels (*Mytilus edulis* L.) from eelgrass (*Zostera marina*) meadows in Maine, U.S.A. Journal of Experimental Marine Biology and Ecology, 394, 45–52.

Ojeda, F.P., Dearborn, J.H., 1989. Community structure of macroinvertebrates inhabiting the rocky subtidal zone in the Gulf of Maine: Seasonal and bathymetric distribution. Marine Ecology Progress Series, 57, 147–161.

Olsson, O., Rogers, D.J., 2009. Predicting the distribution of a suitable habitat for the white stork in Southern Sweden: identifying priority areas for reintroduction and habitat restoration. Animal Conservation, 12, 62–70.

Ompi, M., 2010. Settlement behaviour and size of mussel larvae from the family Mytilidae (*Brachidontes erosus* (Lamarck, 1819), *Brachidontes rostratus* (Dunker, 1857), *Trichomya hirsutus* (Lamarck , 1819), and *Mytilus galloprovincialis* Lamarck , 1819. Journal of Coastal Development, 13, 215–227.

O'Rourke, F., 2010. Tidal energy update 2009. Applied Energy, 87, 398–409.

Phillips, S., Anderson, R., Schapire, R., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling, 190, 231–259.

Phillips, S.J., Dudlik, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31, 161–175.

Pope, S.B., 2000. Turbulent flows. Cambridge University Press, Cambridge.

Powers, S.P., Peterson, C., Grabowski, J., Lenihan, H.S., 2009. Success of constructed oyster reefs in no-harvest sanctuaries: implications for restoration. Marine Ecology Progress Series, 389, 159–170.

Ragnarsson, S. A., Burgos, J.M., 2012. Separating the effects of a habitat modifier, *Modiolus modiolus* and substrate properties on the associated megafauna. Journal of Sea Research, 72, 55–63.

Rees, E.I.S., 2009. Background document for *Modiolus modiolus* beds. OSPAR Commission Biodiversity Series. OSPAR Commission, London.

Rees, E.I.S., Sanderson, W.G., Mackie, A.S.Y., Holt, R.H.F., 2008. Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. III. Crevice, sediment infauna and epifauna from targeted cores. Journal of the Marine biological Association of the United Kingdom, 88, 151 –156.

Roberts, D., Allcock, A.L., Fariñas-Franco, J.M., Gorman, E., Maggs, C., Mahon, A.M., Smyth, D., Strain, E., Wilson, C.D., 2011. *Modiolus* Restoration Research Project: Final Report and Recommendations. Queen's University Belfast, Belfast.

Roberts, D., Davies, C., Mitchell, A., Moore, H., Picton, B., Portig, A., Preston, S.J., Service, M., Smyth, D., Strong, D., Vize, S., 2004. Strangford Lough Ecological Change Investigation (SLECI). Report to Environment and Heritage Service. Queen's University, Belfast.

Robins, P.E., Neill, S.P., Giménez, L., 2012. A numerical study of marine larval dispersal in the presence of an axial convergent front. Estuarine, Coastal and Shelf Science, 100, 172–185.

Rodi, W., 1993. Turbulence models and their application in hydraulics. state of the art review. Special IHR Publication. International Association of Hydraulic Research (Ed.), third ed., A.A. Balkema, Rotterdam.

Rowell, T., 1967. Some aspects of the ecology, growth and reproduction of the horse mussel (*Modiolus modiolus*). Unpublished M. Sc. Thesis, Queens University, Kingston, Ontario.

Schulte, D.M., Burke, R.P., Lipcius, R.N., 2009. Unprecedented restoration of a native oyster metapopulation. Science, 325, 1124.

Seed, R., Brown, R.A., 1975. The influence of reproductive cycle, growth, and mortality on population structure in *Modiolus modiolus* (L.), *Cerastoderma edule* (L.) and *Mytilus edulis* L.,(Mollusca:Bivalvia). In: Barnes, H. (Ed.), 9th European Marine Biology Symposia. Aberdeen University Press, Aberdeen, pp. 257–274.

Seed, R., Brown, R.A., 1978. Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. The Journal of Animal Ecology, 47, 283–292.

Seed, R., Suchanek, T.H., 1992. Population and community ecology of *Mytilus*. In: Gosling, E. (Ed.), The mussel *Mytilus*: ecology, physiology, genetics and culture. Elsevier, Amsterdam, pp. 87-169.

Service, M., Durrant, A., Mills, J., 1996. The trophic status of two northern Irish Sea loughs. Journal of Coastal Conservation, 2, 159–158.

Service, M., Magorrian, B.H., 1997. The extent and temporal variation of disturbance to epibenthic communities in Strangford Lough, Northern Ireland. Journal of the Marine biological Association of the United Kingdom, 77, 1151–116.

Strain, E.M.A., Allcock, A.L., Goodwin, C.E., Maggs, C.A., Picton, B.E., Roberts, D., 2012. The long-term impacts of fisheries on epifaunal assemblage function and structure, in a Special Area of Conservation. Journal of Sea Research, 67, 58–68.

Taylor, J., Service, M., 1997. The trophic status of Strangford Lough. Department of Agriculture of Northern Ireland, Belfast.

Tendal, O.S., Dinesen, G.E., 2005. Biogenic sediments, substrates and habitats of the Faroese shelf and slope. BIOFAR Proceedings 2005, 224–242.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews, 25, 1-45.

Wildish, D.J., Fader, G.B.J., Lawton, P., MacDonald, A.J., 1998. The acoustic detection and characteristics of sublittoral bivalve reefs in the Bay of Fundy. Continental Shelf Research, 18, 105–113.

Wilson, C.D., Roberts, D., Reid, N., 2010. Applying species distribution modelling to identify areas of high conservation value for endangered species: A case study using *Margaritifera margaritifera* (L.). Biological Conservation 144, 821–829.

Wilson, C.D., Arnott, G., Reid, N., Roberts, D., 2011. The pitfall with PIT tags: marking freshwater bivalves for translocation induces short-term behavioural costs. Animal Behaviour, 81, 341–346.

Witman, J.D., 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. Ecological Monographs, 55, 421–445.

Witman, J.D., 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. Ecological Monographs, 57, 167–187.

Yang, Z., Sobocinski, K.L., Heatwole, D., Khangaonkar, T., Thom, R., Fuller, R., 2010. Hydrodynamic and ecological assessment of nearshore restoration: A modeling study. Ecological Modelling, 221, 1043–1053.

Figure captions

Fig. 1. Map of Strangford Lough, Northern Ireland and enlarged surveyed area showing current *M. modiolus* reef positions (black dots) and model release sites 1. Hadd Rock; 2. Craigyouran; 3. Round Island Pinnacle; 4. Black Rock; and 5. Restoration site. Rectangles indicate Sea Fisheries Exclusion Zones implemented in March 2011. The intertidal zone is represented in grey.

Fig. 2. Predicted particle distribution after 56 days from 5 different release points. A: Irish Sea; B: Black Rock; C: Black Rock with wind dispersion; D: Craigyouran and Round Island Pinnacle. E: Hadd Rock. Release of particles is constant simulating trickle spawning, timestep 5 minutes, 200 particles per timestep.

Fig. 3. Predicted effect of reef elevation on particle distribution from the restoration site after 56 days: A) 0.1 m; B) 0.25 m; C) 0.5 m; and D) 1 m. Release of particles is constant simulating trickle spawning, timestep 5 minutes, 200 particles per timestep.

Fig. 4. Mean velocity at seabed due to wave action for a 6 week autumn period (September – October 2010) at the 5 different release sites compared with a near shore bed site (note logarithmic scale).

Fig. 5. Comparison of mean concentration of particles on the restoration site with the north and south reef 300 and 150 m in the current direction for both ebb and flood currents, with a release at 0.01, 0.25, 0.5 and 1 m from the bed with 1 million larvae released

Fig. 6. Jackknife analyses of the importance of environmental variables in maximum entropy modelling of *M. modiolus* occurrence in Strangford Lough. A heuristic estimate of the relative contribution of each variable to the global model is given in parentheses whilst variables are listed in descending order of importance. Grey bars show the performance of the global model (known as test gain) without each variable and black bars show the influence of each variable in isolation (derived from a univariate model only).

Fig. 7. Marginal response curves of the predicted probability of *M. modiolus* occurrence (*y*-axis) in Strangford Lough, for explanatory variables that contributed substantially to the global maximum entropy model. *X*-axes represent percentage cover for each substrate type and meters below surface for depth.

Fig. 8. (A) Habitat favourability model for *M. modiolus* throughout Strangford Lough, Northern Ireland, UK, providing a means by which to identify areas of high conservation value for the species. (B) Historical distribution of *M. modiolus* in Strangford Lough based on cumulative site-specific records (black squares) (Roberts et al., 2004).

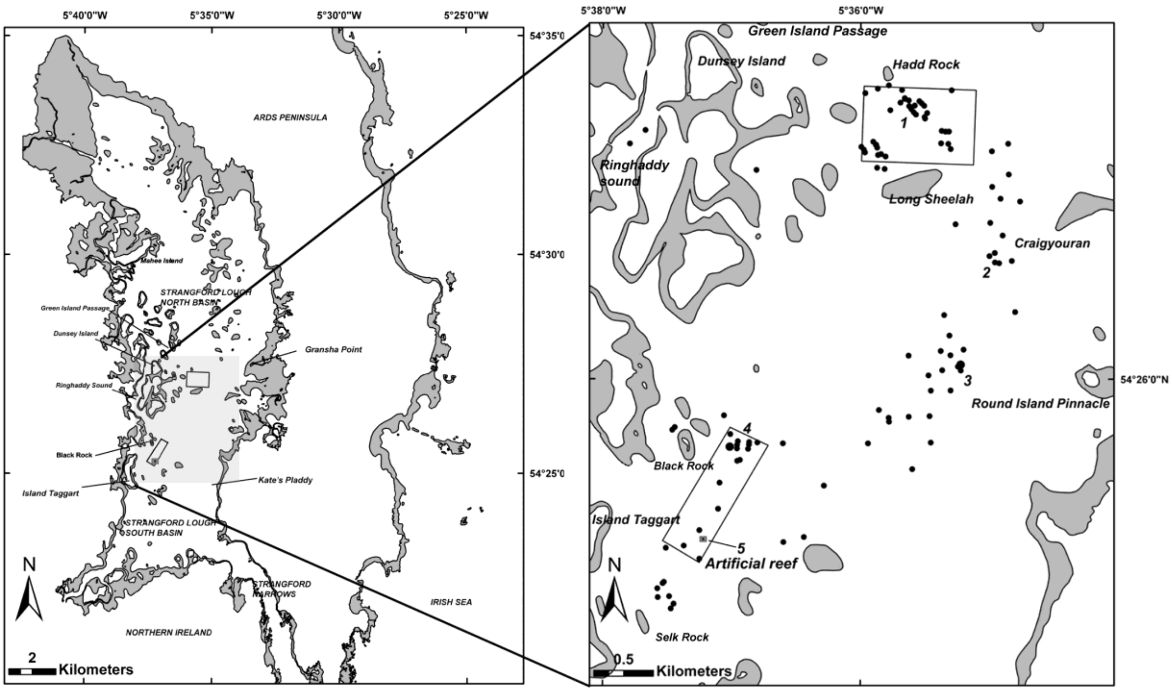
5°40'0"W
5°35'0"W
5°30'0"W
5°25'0"W
54°35'0
54°30'0
54°25'0
ARDS PENINSULA
Mahee Island
STRANGFORD LOUGH NORTH BASIN
Green Island Passage
Dunsey Island
Gransha Point
Ringhaddy Sound
Black Rock
Island Taggart
Kate's Pladdy
STRANGFORD LOUGH SOUTH BASIN
STRANGFORD NARROWS
IRISH SEA
NORTHERN IRELAND
N
2
Kilometers
5°38'0"W
5°36'0"W
Green Island Passage
Dunsey Island
Hadd Rock
1
Ringhaddy sound
Long Sheelah
Craigyouran
2
3
54°26'0"N
Round Island Pinnacle
4
Black Rock
Island Taggart
5
Artificial reef
Selk Rock
0.5
Kilometers

Fig. 1

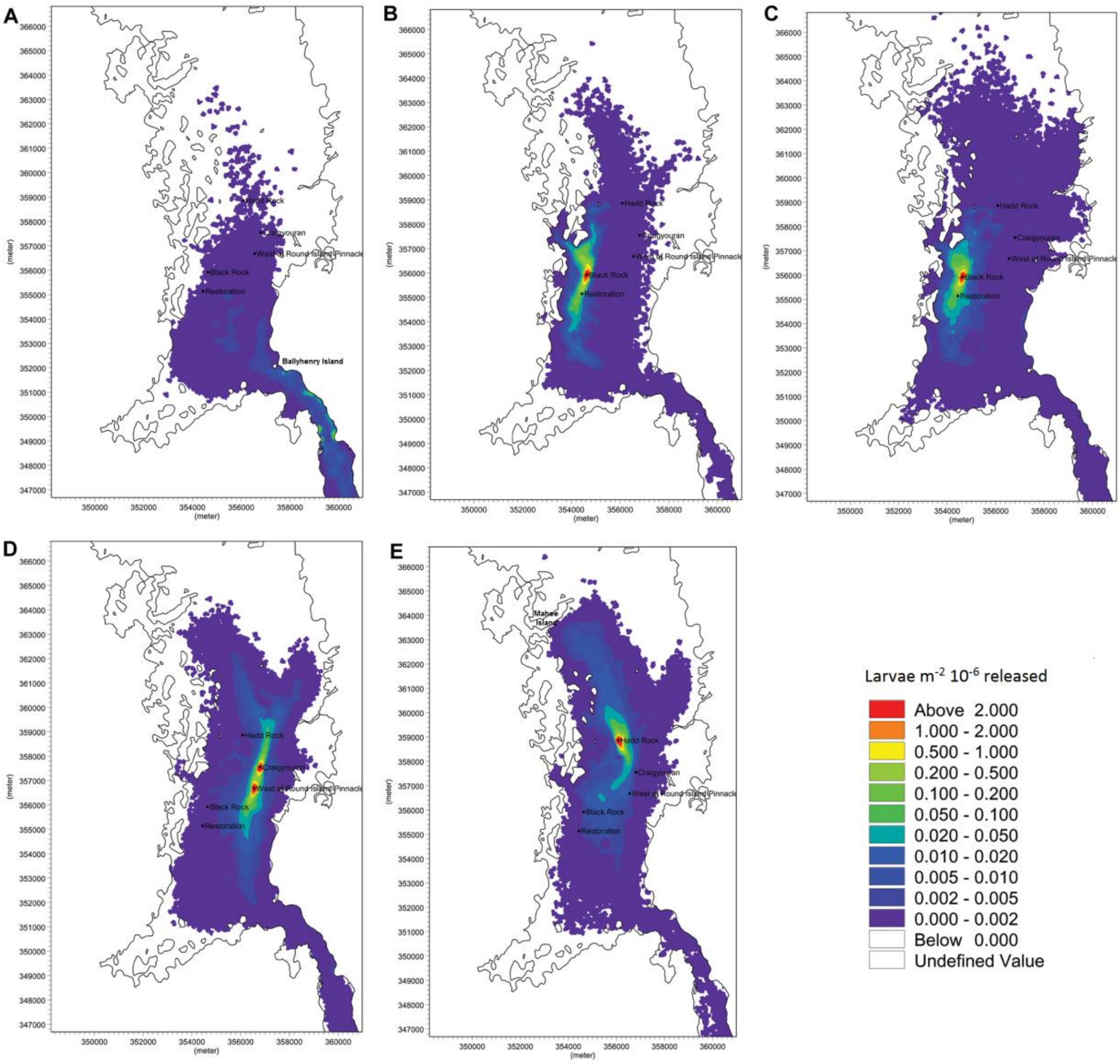
A
B
C
D
E
Hadd Rock
Craigyouran
West of Round Island Pinnacle
Black Rock
Restoration
Ballyhenry Island
Mahee Island
(meter)
Larvae m-2 10-6 released
Above 2.000
1.000 - 2.000
0.500 - 1.000
0.200 - 0.500
0.100 - 0.200
0.050 - 0.100
0.020 - 0.050
0.010 - 0.020
0.005 - 0.010
0.002 - 0.005
0.000 - 0.002
Below 0.000
Undefined Value

Fig. 2

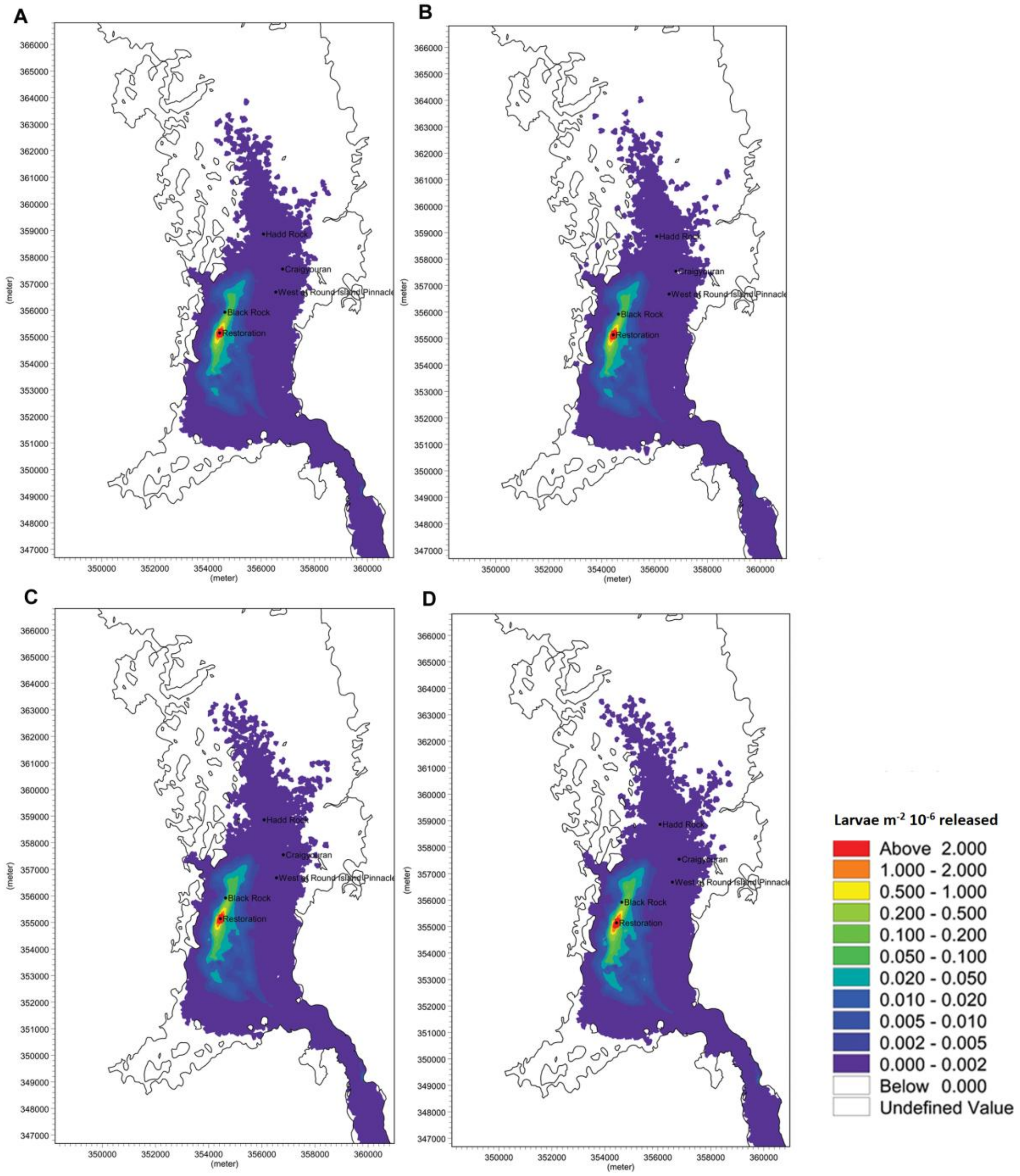
A
B
C
D
Hadd Rock
Craigyouran
West of Round Island Pinnacle
Black Rock
Restoration
(meter)
Larvae m-2 10-6 released
Above 2.000
1.000 - 2.000
0.500 - 1.000
0.200 - 0.500
0.100 - 0.200
0.050 - 0.100
0.020 - 0.050
0.010 - 0.020
0.005 - 0.010
0.002 - 0.005
0.000 - 0.002
Below 0.000
Undefined Value

Fig. 3

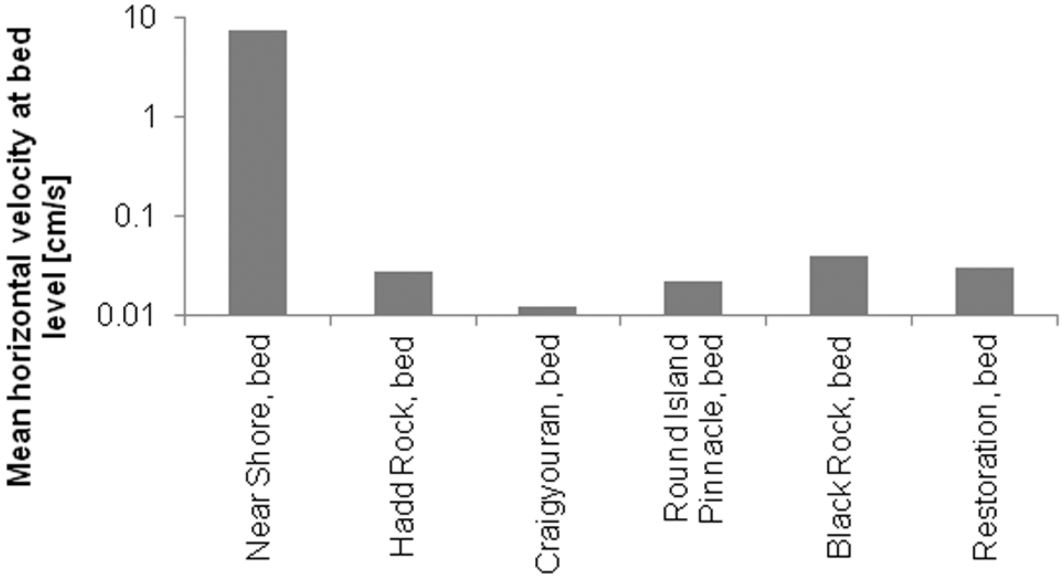
Mean horizontal velocity at bed level [cm/s]
10
1
0.1
0.01
Near Shore, bed
Hadd Rock, bed
Craigyouran, bed
Round Island Pinnacle, bed
Black Rock, bed
Restoration, bed

Fig. 4

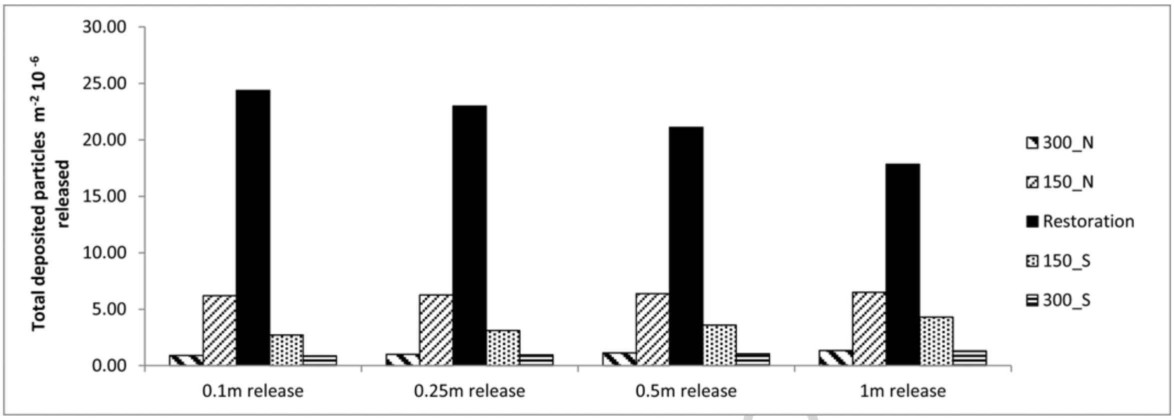
30.00
25.00
20.00
15.00
10.00
5.00
0.00
Total deposited particles m^{-2} 10^{-6} released
0.1m release
0.25m release
0.5m release
1m release
300_N
150_N
Restoration
150_S
300_S

Fig. 5

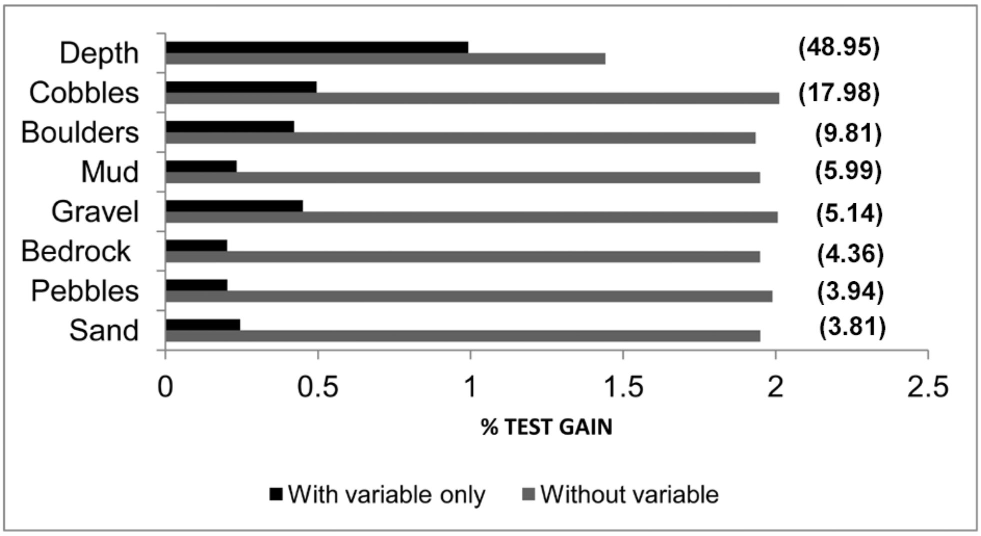
Depth
Cobbles
Boulders
Mud
Gravel
Bedrock
Pebbles
Sand
(48.95)
(17.98)
(9.81)
(5.99)
(5.14)
(4.36)
(3.94)
(3.81)
0
0.5
1
1.5
2
2.5
% TEST GAIN
With variable only
Without variable

Fig. 6

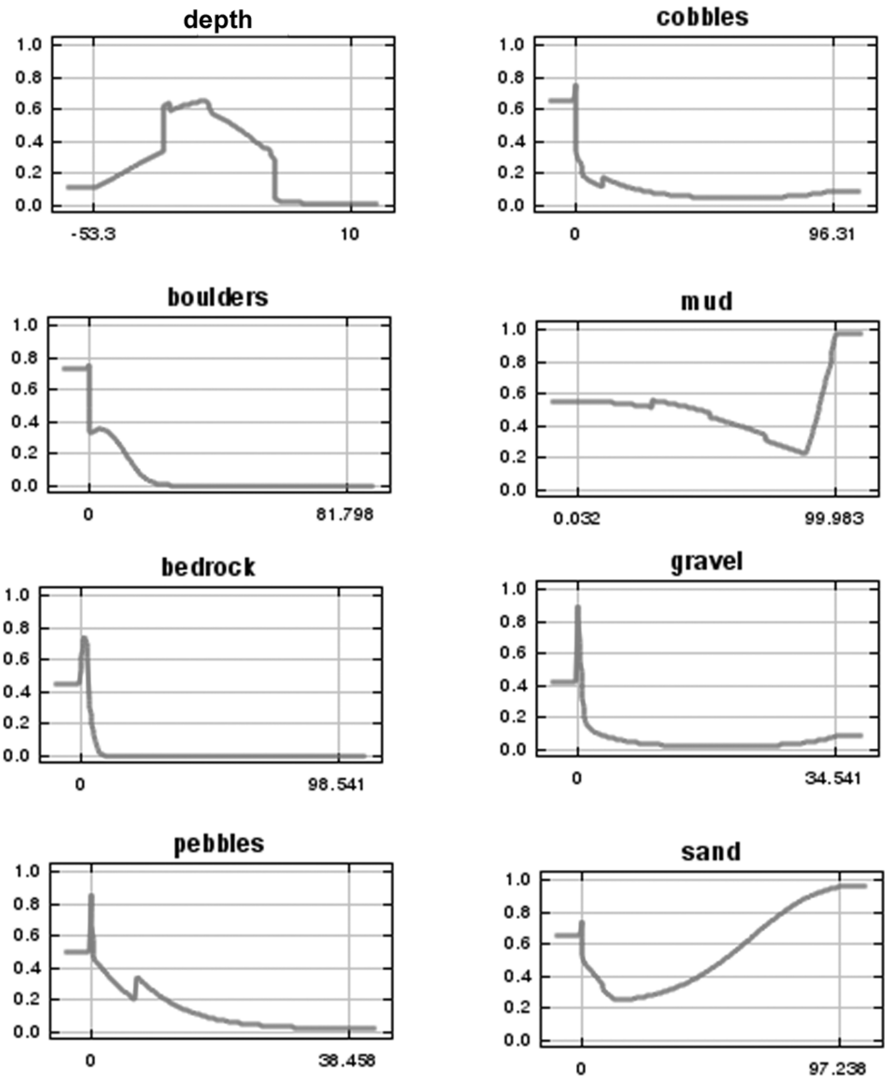
depth
1.0
0.8
0.6
0.4
0.2
0.0
-53.3
10
cobbles
96.31
0
boulders
0
81.798
mud
0.032
99.983
bedrock
0
98.541
gravel
0
34.541
pebbles
0
38.458
sand
0
97.238

Fig. 7

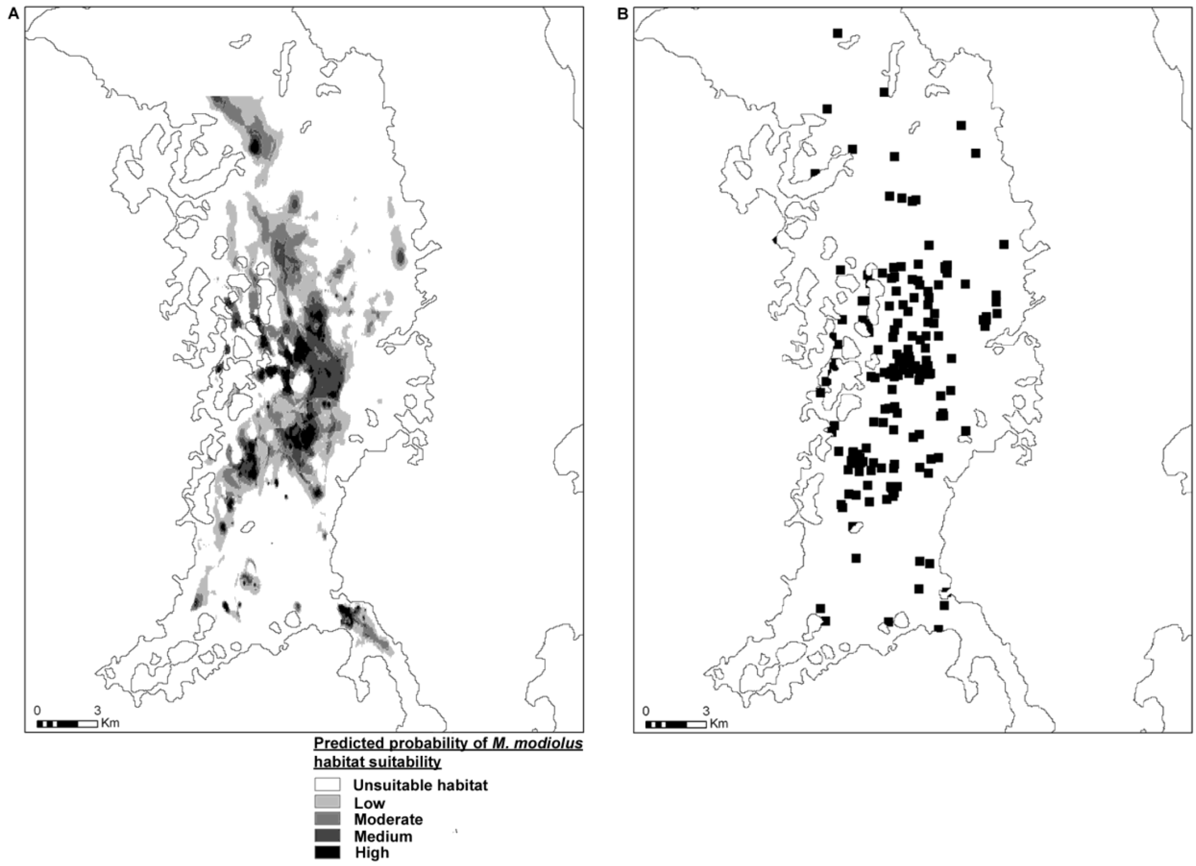
A
0
3
Km
Predicted probability of M. modiolus habitat suitability
Unsuitable habitat
Low
Moderate
Medium
High
B
0
3
Km

Fig. 8

Highlights

- Strangford Lough is a sink for larvae
- Remaining populations are self-recruiting
- There is little or no connectivity between the beds
- North South currents are a barrier for larval dispersal between East and West.